

# Distribution of ostracods in west-central Argentina related to host-water chemistry and climate: implications for paleolimnology

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Received: 6 October 2016 / Accepted: 24 March 2017  
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**Abstract** Ecological and biogeographical studies of Neotropical non-marine ostracods are rare, although such information is needed to develop reliable paleoecological and paleoclimatic reconstructions for the region. An extensive, yet little explored South American area of paleoclimatic interest, is the arid-semiarid ecotone (Arid Diagonal) that separates arid Patagonia from subtropical/tropical northern South America, and lies at the intersection of the Pacific and Atlantic atmospheric circulation systems. This study focused on the Laguna Llanquanelo basin, Argentina, a Ramsar site located within the Arid Diagonal, and was designed to build a modern dataset using ostracods (diversity, spatial distribution, seasonality, habitat preferences) and water chemistry. Cluster and

multivariate analysis of the data indicated that salinity is the most significant variable segregating two ostracod groups. *Limnocythere* aff. *staplini* is the only species that develops abundant populations in the saline ephemeral Laguna Llanquanelo during almost all seasons, and is accompanied by scarce *Cypridopsis vidua* in summer. The latter species is abundant in freshwater lotic sites, where *Ilyocypris ramirezi*, *Herpetocypris helenae*, and Cyprididae indet. are also found in large numbers. *Darwinula stevensoni*, *Penthesilenula incae*, *Heterocypris incongruens*, *Chlamydotheca arcuata*, *Chlamydotheca* sp., *Herpetocypris helenae*, and *Potamocypris smaragdina* prefer freshwater lentic conditions (springs), with *C. arcuata* and *Chlamydotheca* sp. found only in the Carapacho warm spring, which has a year-round constant temperature of ~20 °C. Seasonal sampling was necessary because some taxa display a highly seasonal distribution. Species that were recorded

**Electronic supplementary material** The online version of this article (doi:[10.1007/s10933-017-9963-1](https://doi.org/10.1007/s10933-017-9963-1)) contains supplementary material, which is available to authorized users.

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have either subtropical or Patagonian affinities, although a few taxa are endemic or common to both regions. These data can serve as modern analogues for reconstructing the late Quaternary history of the area, and to investigate the extent and position of the arid/semiarid ecotone (Arid Diagonal) during past glacial/interglacial cycles.

**Keywords** Non-marine ostracods · *Limnocythere* · Laguna Llanquanelo · Arid Diagonal · South America · Paleoclimate

## Introduction

Ecological and biogeographical studies of non-marine ostracods from the Neotropical bioregion are rare, despite the wide application of ostracods in paleoclimate and paleoecological reconstructions. Databases such as the European (OMEGA, Horne et al. 2011) and North America databases (NACODE: North America Combined Ostracode Database; originally named NANODE (North American Non-marine Ostracode Database) (Forester et al. 2005; Curry et al. 2012) are compiling data on the presence/absence of ostracod species and associated hydrological/geochemical and climate conditions, to develop calibration datasets for paleo-reconstructions. The effort to build comprehensive databases will not be complete until data from the Southern Hemisphere are incorporated, particularly from South America, where the number of recorded ostracod species is low compared to other continents, including Australia and Africa (Martens et al. 2008).

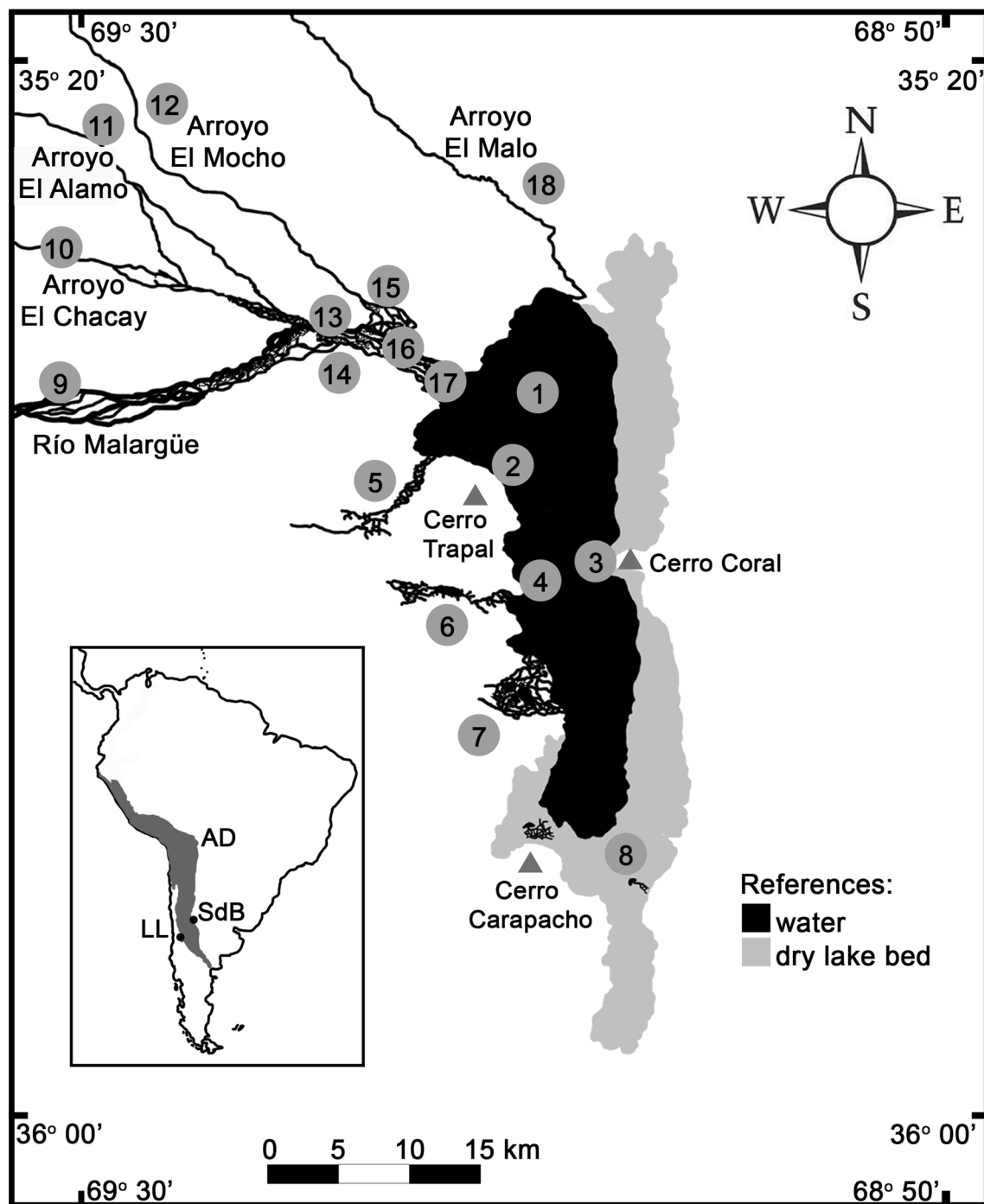
Ostracod assemblages are useful to determine past hydrological conditions [salinity, temperature, water energy (De Deckker and Forester 1988; Curry 1999)] and water depth (Mourguiart et al. 1998), and when coupled with trace-element and oxygen-isotope analyses, enable estimation of past salinity, temperature and pH conditions (Chivas et al. 1983, 1985, 1986a, b; Gouramanis et al. 2010). In Argentina, Schwalb et al. (2002) studied ostracod taxa and isotopes from two Patagonian lakes, providing a database that can be applied to paleo-reconstructions. Other recent papers, involving a variety of approaches, have been published on studies in Patagonia (Cusminsky et al. 2005, 2011; Ballent and Díaz 2011; Ramón Mercau et al. 2012), the Pampas inland and coastal wetlands, including Isla

Martín García, eastern Argentina (Cusminsky et al. 2006; Liberto et al. 2012; Ramón Mercau et al. 2014), and the Altiplano of northern Argentina (Laprida et al. 2006; Díaz and Lopretto 2011; Palacios-Fest et al. 2016). As part of this project in central-western Argentina, D'Ambrosio et al. (2015, 2016a) published a description of the soft parts of *Ilyocypris ramirezi* Cusminsky and Whatley (1996), a taxon originally described from Patagonian Quaternary sediments using only hard parts, and a revised description of *Herpetocypris helenae* Müller, 1908, which included soft and hard parts and was reported for the first time in the Neotropical region.

This study focuses on ostracods and water chemistry from a system of wetlands in west-central Argentina, namely the Laguna Llanquanelo basin (~35° S Lat), located about 70 km east of the Andes range, where the mountains produce a topographic barrier that restricts continued easterly flow of winds and humidity. This situation changes south of ~40° S latitude, where the altitude of the Andes diminishes and the westerlies from the Pacific Ocean are the dominant wind through Patagonia, reaching the Pampean area. The wetlands are within the Arid Diagonal (Bruniard 1982), an extensive semiarid-arid area that receives <250 mm of annual precipitation, and that traverses South America approximately following the Río Colorado-Desaguadero basins in Argentina and continuing northwest to northern Perú (Fig. 1). Northeast of the Arid Diagonal the climate is subtropical, with annual precipitation >600 mm, mostly affected by the Atlantic Ocean summer monsoon. South of the Arid Diagonal the climate is arid, with annual precipitation <200 mm, typical of Patagonia, and influenced by the Pacific Ocean (Piovano et al. 2009).

Modern ecological studies from the wetlands connected to Laguna Llanquanelo dealt with malacofauna (Ciocco and Scheibler 2008; Scheibler and Ciocco 2011, 2013), plankton (Peralta and Fuentes 2005; D'Ambrosio et al. 2016b) and the ostracods *I. ramirezi* (D'Ambrosio et al. 2015) and *H. helenae* (D'Ambrosio et al. 2016a). Paleolimnological research undertaken at other sites within the Arid Diagonal (Salina del Bebedero and Río Atuel) used charophytes (García 1999) and molluscs (De Francesco 2010; De Francesco and Hassan 2009).

This is the first comprehensive study of ostracod diversity, water chemistry and seasonal data from the



**Fig. 1** Location of sampling sites in Mendoza province, Argentina. 1–4 Laguna Llancanelo (Llancanelo Lake), 5 Bañado Los Menucos (Los Menucos spring), 6 Bañado Carilauquen (Carilauquen spring), 7 Bañado Carapacho (Carapacho warm spring), 8 Bañado La Porteña (La Porteña spring), 9 Río Malargüe (Malargüe River), 10 Arroyo El Chacay (El

Chacay creek), 11 Arroyo El Alamo (El Alamo creek), 12 Arroyo El Mocho (El Mocho creek), 13–17 Delta del Río Malargüe (Malargüe River delta), 18 Arroyo El Malo (El Malo creek). In the *inset map* of South America, LL is the position of Laguna Llancanelo, SdB is Salina del Bebedero (San Luis province) and the *shaded grey area* (AD) is the Arid Diagonal

distinctive ecosystems of the Laguna Llancanelo area. This modern dataset provides ostracod/environment relationships across a broad environmental gradient, and is applicable to reconstruction of paleoecological and paleoclimate conditions in wetlands from the Arid Diagonal and elsewhere. The dataset also has the potential to shed light on changes in the behaviour of this ecotone during glacial/interglacial times, in response to weakening or strengthening of Pacific or Atlantic atmospheric circulation patterns.

A larger paleolimnological project in the Llancanelo area is currently being completed, including geochemistry of modern and fossil ostracod valves. Cores obtained in the lake basin are up to 10 m long and span the past 30 ka. Results from continuing “paleo” studies will be published separately and are beyond the scope of this paper.

#### Study site

The Llancanelo wetlands are located in southwest Mendoza Province, Argentina (35°–36.5°S, 68.5°–70°W) at 1330 m a.s.l., and close to the Cordillera de los Andes (Fig. 1). The drainage basin is endorheic, developed within the Huarpes depression in the northern section of the Payenia Volcanic Province (Ramos and Folguera 2011), an area characterized by the presence of more than 800 back-arc volcanic cones, some as young as 5 ka. Input of volcanic ash in the area, however, commonly derives from the Cordillera de los Andes, and layers of volcanic ash are found in the banks of creeks and around springs.

#### Sampling sites

Eighteen localities in the Laguna Llancanelo area were selected for sampling, but two sites were consistently dry (Arroyo El Alamo and Arroyo El Malo), so 16 sites (lotic, lentic, temporary, permanent, fresh to mesosaline ecosystems) were sampled seasonally for water and ostracod analyses (Fig. 1, Electronic Supplementary Material [ESM] Table S1).

#### *Lentic, permanent, fresh and saline environments*

Laguna Llancanelo (Fig. 1, sites 1–4) is a Provincial Reserve and a Ramsar site because of its important ecological role. It is the largest wetland within the

arid area north of Patagonia, a refuge for endemic flora and fauna, and the nesting site for large colonies of flamingoes. The lake is ephemeral, shallow and saline, with a mean water depth of 0.3–1.7 m. Its surface area is ~28,000 ha, with large changes in lake area at annual, inter-annual and decadal scales (Isla et al. 2005). The lake is fed by permanent and ephemeral streams, groundwater and cold and warm springs—all fresh. The principal water source is from Andean snowmelt in spring and comes mainly from the Malargüe River.

According to Ostera and Dapeña (2003) the water is a chloride–sulfate–sodium type, with mean conductivity of 10.8 mS cm<sup>−1</sup> (Peralta and Fuentes 2005). The high temperature and scarce rainfall produce salt flats in the shallowest areas of the lake.

There are several types of springs (bañados) around the lake (Fig. 1, sites 5–8). These are developed in depressions where groundwater emerges and forms large wetlands, commonly connected to the lake by small streams. Los Menucos rheocene spring (site 5) is located in the northwest of the lake and has a mean water depth of 0.3 m. Carilauquen limnocene spring (site 6) is located southwest of the lake; the water is predominantly sulfate calcic and has a mean conductivity of 0.959 mS cm<sup>−1</sup> (Peralta and Fuentes 2005) and mean water depth of 0.2 m, though deeper areas reach 1.6 m (Ciocco and Scheibler 2008). The Carapacho helocene spring (site 7) is the only warm spring in the area, located on the southwest side of the lake. The spring's temperature is constant during the four seasons, around 19–20 °C; this is also the deepest wetland in the area, up to 4 m deep, although the mean water depth is 1 m and sampling was done close to the shore. La Porteña limnocene spring (site 8) is in the southeast part of the lake, with a mean water depth of 0.5 m.

#### *Lotic permanent environments*

Río Malargüe (site 9) originates in the Cordillera de los Andes at 3000 m a.s.l. and receives input from numerous tributaries as it flows to Laguna Llancanelo, producing maximum discharge in spring and summer. Arroyo El Chacay (site 10) is a creek that originates in the Andes and flows eastward, joining the Río Malargüe close to the lake.

### *Lotic temporary environments*

Arroyo El Alamo (site 11) is a tributary of Arroyo El Chacay and was dry during the sampling period. Accordingly, there are no data from this site. Arroyo El Mocho (site 12) originates in the Andes, and is a second-order tributary of the Río Malargüe, joining it in the lower section of its course. This creek displayed highly variable inter-season flow during sampling, holding much water during autumn and winter, but being almost dry in summer. The Río Malargüe delta (sites 13–17) forms where this river joins the lake in its northwest corner, after receiving water from Arroyos El Chacay and El Mocho. The delta is developed in a lowland area known as “Bajo Llanecanelo” and holds water only temporarily because of marked seasonal fluctuations. Arroyo El Malo (site 18), which used to discharge into the northeast section of the lake, is now permanently dry, although it was an important watercourse in the past, its paleo-channel showing a connection to the Río Salado, which runs toward the north of the Llanecanelo basin.

## Materials and methods

### Sampling procedures

Samples of ostracods and water were taken seasonally from 16 sites (September 2009–September 2010), and several physical and chemical variables of the waters were measured in situ at the same time. Ostracod samples were collected in shallow areas (about 20–40 cm deep) by washing aquatic plants (three times at each site to recover ostracod species that live close to macrophytes) and surrounding surface sediments (upper 3 cm) in a bucket, then rinsing the sediments in a 100- $\mu$ m sieve. Samples were divided in two aliquots, one stored in 70% ethanol and the other air-dried.

In the field, a Horiba U-10 multimeter was used to measure pH, temperature, dissolved oxygen (DO) and conductivity. To calculate salinity, the conversion table from conductivity (envco) was used. Salinity classification used the ranges and terms proposed by Hammer et al. (1983).

Water samples were collected in bottles (500 ml) from the water surface, avoiding bubbling, after rinsing the bottles with water of the corresponding wetland. Once hermetically sealed, the bottles were stored in darkness and kept cold (4 °C). In the Geochemistry Laboratory, University of Wollongong, Australia, the water was filtered at 2.5  $\mu$ m retention (Filtech 1803), and kept in bottles pre-washed with 10% HNO<sub>3</sub> prior to chemical analysis using an Agilent 7500 ce Inductively Coupled Plasma Mass Spectrometer (ICP-MS). The interference-free isotopes <sup>48</sup>Ca, <sup>86</sup>Sr, <sup>25</sup>Mg, <sup>39</sup>K and <sup>138</sup>Ba were analyzed.

### Ostracod assemblage analyses

In the laboratory, each dried sample was washed again with tap water on a 100- $\mu$ m sieve. Given the paleolimnological objectives of this work, we focused on detailed study of the hard parts, valves and carapaces, as these are the only parts of the ostracod that preserve in sediments and form the basis for the taxonomy of fossil taxa. Carapaces and valves were inspected using a stereo-microscope to separate those in perfect condition (in some cases with soft parts still attached), from those showing signs of dissolution or transport. Only ostracods showing pristine preservation were counted to be sure that specimens were either alive at the time of collection or had died very recently. The ostracods were sorted and valves stored dry on micro-paleontological slides. Identification at the genus and species level was performed using local literature and general references commonly used for ostracod systematics, with the abbreviations Cp (carapace), dv (dorsal view), ev (external view), H (height of valve), iv (internal view), lv (lateral view), L (length of valve), LV (left valve), RV (right valve), and vv (ventral view) used for descriptions of the valves. Valves were photographed and measured using scanning electron microscopy (SEM) (JEOL JSM 6360 LV at Universidad Nacional de La Plata, JEOL JSM 6610 LV at IANIGLA, Mendoza, Argentina, Philips XL30 at Royal Belgian Institute of Natural Sciences, Brussels, Belgium and JEOL JSM 6490 LA at University of Wollongong, Australia). The material is deposited in the carcinological collection of the Museo de La Plata,

La Plata (Argentina) (MLP numbers). For statistical analyses, samples were standardized as individuals per gram of dry sediment.

Database: ostracods, environmental variables and water chemistry

Construction of a modern database, using data from the Llanccanelo area, included sampling sites with geo-referenced positions, ecological variables (pH, salinity, conductivity, DO, temperature), and chemical analysis of the water (Ba, Ca, Mg, Na, Sr, K), collected seasonally (Table S1, ESM).

#### Statistical analyses

To explore relationships between ostracod associations and each type of environment, cluster analyses, outlined by constrained incremental sum of squares analysis and unconstrained-type analysis and square root transformation (CONISS), were carried out using Tilia and TiliaGraph programs (TGView 2.0.2; Grimm 2004). In addition, similarity analysis was used to segregate environmental variables that control the distribution of ostracods.

To investigate the relationship between species composition and environmental variables over the studied period, multivariate ordination techniques from the CANOCO program (version 4.5) were used (Pielou 1984; ter Braak 1986). The method of redundancy analysis (RDA) was selected because the lengths of the gradients of explanatory variables were short (ter Braak and Smilauer 2002).

Redundancy Analysis (RDA) was implemented to investigate which environmental and water chemistry factors affected ostracod distribution, with the analyses including only those environmental variables with a variance inflation smaller than 10, to mitigate the effect of multi-collinearity (ter Braak and Verdonschot 1995). The environmental data were standardized, then 11 ostracod species and 11 environmental variables from 16 sites collected in four seasons (72 samples) were statistically analysed. The statistical significance of variability for each parameter, and the general meaning of ordination were tested with a Monte Carlo test (499 permutations,  $p < 0.01$ ), with three variables (salinity, Ba and Sr) being used for the posterior analysis.

## Results

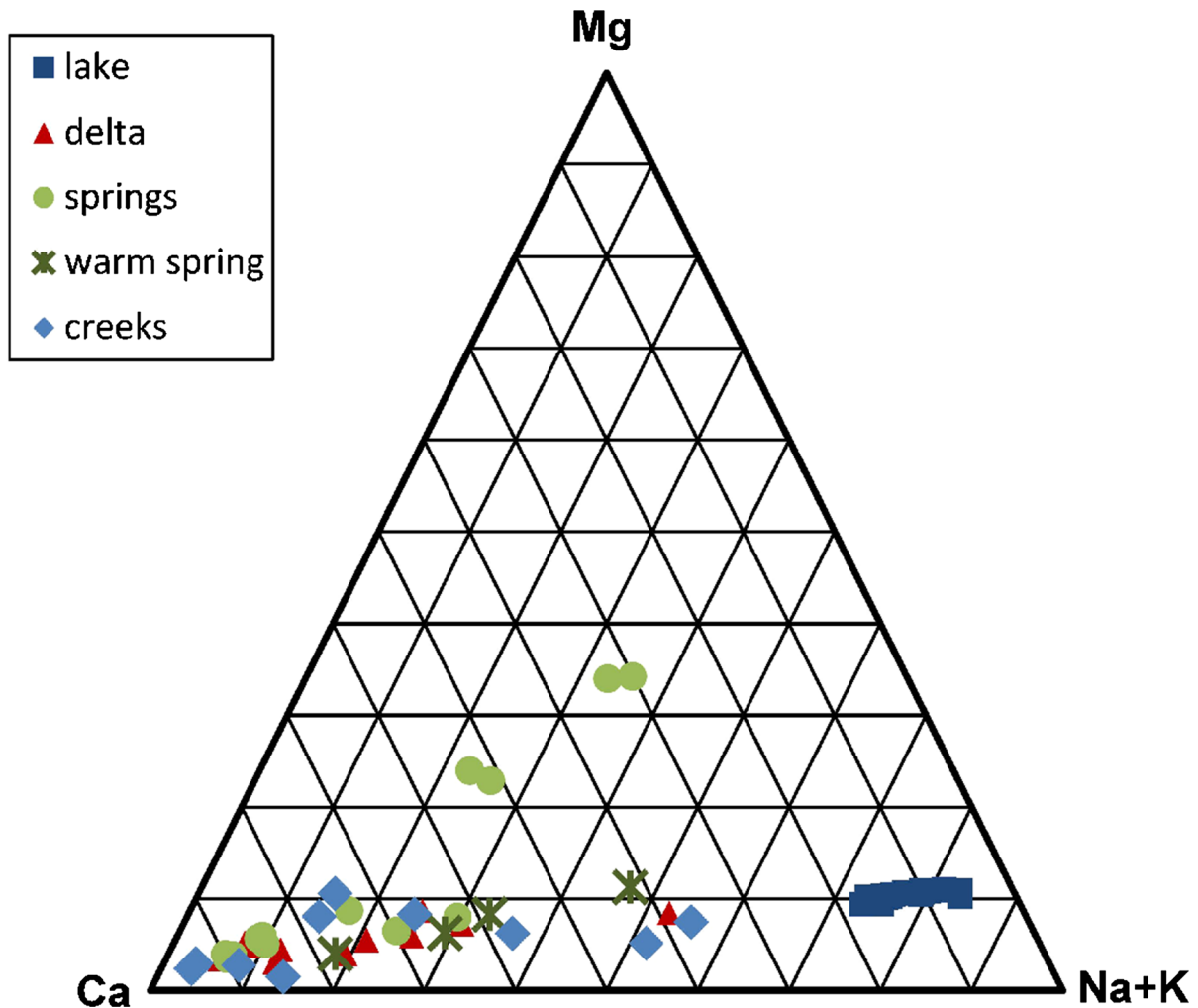
### Water chemistry

The progressive, largely evaporative chemical evolution of the water bodies, from creeks, springs and delta inflow, through to a saline lake, is accompanied by a progressive increase in the relative amount of sodium and potassium, as demonstrated on a cation ternary diagram (Fig. 2) and by total salinity. On this diagram, Carapacho warm spring is similar to the cold springs. La Porteña spring, located on the east side of the lake, is somewhat different, with relatively higher magnesium content in all four sampled seasons. Earlier studies on limited datasets (Ostera and Dapeña 2003; Alvarez and Wetten 2004) demonstrated that anion evolution in water bodies of the Llanccanelo area progresses from high relative levels of dissolved sulfate to high chloride, with a progressive increase in total salinity. The oxygen isotope values (vs VSMOW) of several of the water bodies span a considerable range, consistent with progressive evaporation. Sampling in February 2001, Ostera and Dapeña (2003) showed that the Andean headwaters (3000 m a.s.l.) of the Río Malargüe have a  $\delta^{18}\text{O}$  value of  $-16.5\text{‰}$ , with several springs, including Carilauquen, near Laguna Llanccanelo having values of  $-14.9$  to  $-14.4\text{‰}$ , and Laguna Llanccanelo a value of  $+0.5\text{‰}$ .

The solute chemistry of the various water bodies can be further examined using a series of bivariate diagrams. Sodium and potassium, previously grouped together in the triangular plot, are separated in Fig. 3a. The saline lake water demonstrates conservative consistency, with a molar Na:K ratio of 52, as do the less saline ponds, again except for La Porteña (the four more-saline green dots). Among the saline lakes, the four seasonal samples at Cerro Coral (Na = 550–660) are enriched in Na over K. This part of the lake is also fed by a saline spring at the foot of Cerro Coral, which must be adding additional Na. Similar to La Porteña, this is on the east side of the lake, suggesting that the north–south geological fault that is commonly postulated to be along the eastern shoreline, taps deeper water, rather than just near-surface groundwater and rain water.

Plots of strontium versus calcium (Fig. 3b) and magnesium versus calcium (Fig. 3c) distinguish La Porteña, whereas the saline lake waters demonstrate





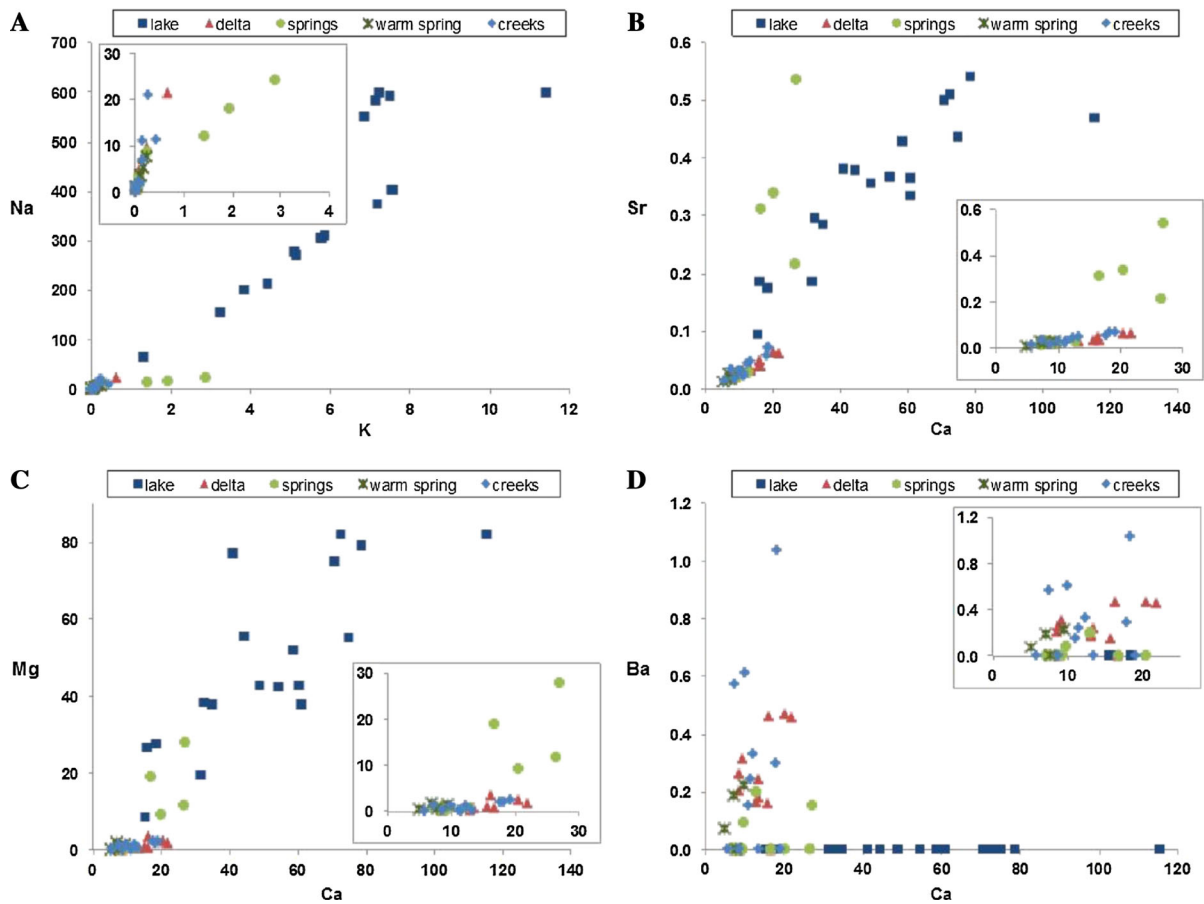
**Fig. 2** Cation diagram, in molar proportions, for solutes from water bodies within the Llançanelo catchment. All four seasonal samples from La Portaña spring plot with a higher relative Mg content, near the *centre of the triangle*

their depleted barium content on a Ba versus Ca diagram (Fig. 3d), as Ba has been precipitated as  $\text{BaSO}_4$  and/or  $\text{BaCO}_3$ , upon reaching saturation for these species. In a later section we examine whether these salinity and water chemistry differences exert control on the ostracod assemblages in each water body.

#### Ostracods

Eleven species of ostracods were identified: *Limnocythere* aff. *staplini* Gutentag and Benson, 1962, *Chlamydotheca arcuata* (Sars, 1901), *Chlamydotheca* sp., *Heterocypris incongruens* (Ramdohr, 1808), *Cypridopsis vidua* (Müller, 1776), *Potamocypris*

*smaragdina* (Vávra, 1891), *Herpetocypris helenae* Müller, 1908, *Ilyocypris ramirezi* Cusminsky and Whatley, 1996, *Darwinula stevensoni* (Brady and Robertson, 1870), *Penthesilenula incae* (Delachaux, 1928) and Cyprididae indet. The description and SEM illustration of *Limnocythere* aff. *staplini* is presented in the main text because it is the characteristic taxon in the Laguna Llançanelo area, particularly in the lake, where a large population consisting of males, females and juveniles was found. The description, environmental preferences, and SEM illustrations of the remaining ostracod taxa are provided in the ESM. The relative abundance of each taxon at each locality in the different seasons is shown in ESM Fig. S2. ESM Table S1 is the



**Fig. 3** Bivariate molar plots (in milliequivalents per litre) of **a** Na versus K, **b** Sr versus Ca, **c** Mg versus Ca, and **d** Ba versus Ca, for waters within the Llançanelo catchment. Within each panel, the inset diagrams expand the scale for the areas near the origin

complete modern database arising from this study, including site names, GPS positions, ostracod taxa, ecological variables and water chemistry data collected seasonally. ESM Table S2 compiles maximum and minimum values of the ecological data for each ostracod taxon.

Class Ostracoda Latreille, 1802

Order Podocopida G. O. Sars, 1866

Superfamily Cytheroidea Baird, 1850

Family Limnocytheridae Klie, 1938

Genus *Limnocythere* Brady, 1867

*Limnocythere* aff. *staplini* Gutentag and

Benson, 1962

(Fig. 4 MLP 27186)

Material: 9750 valves, adults and juveniles.

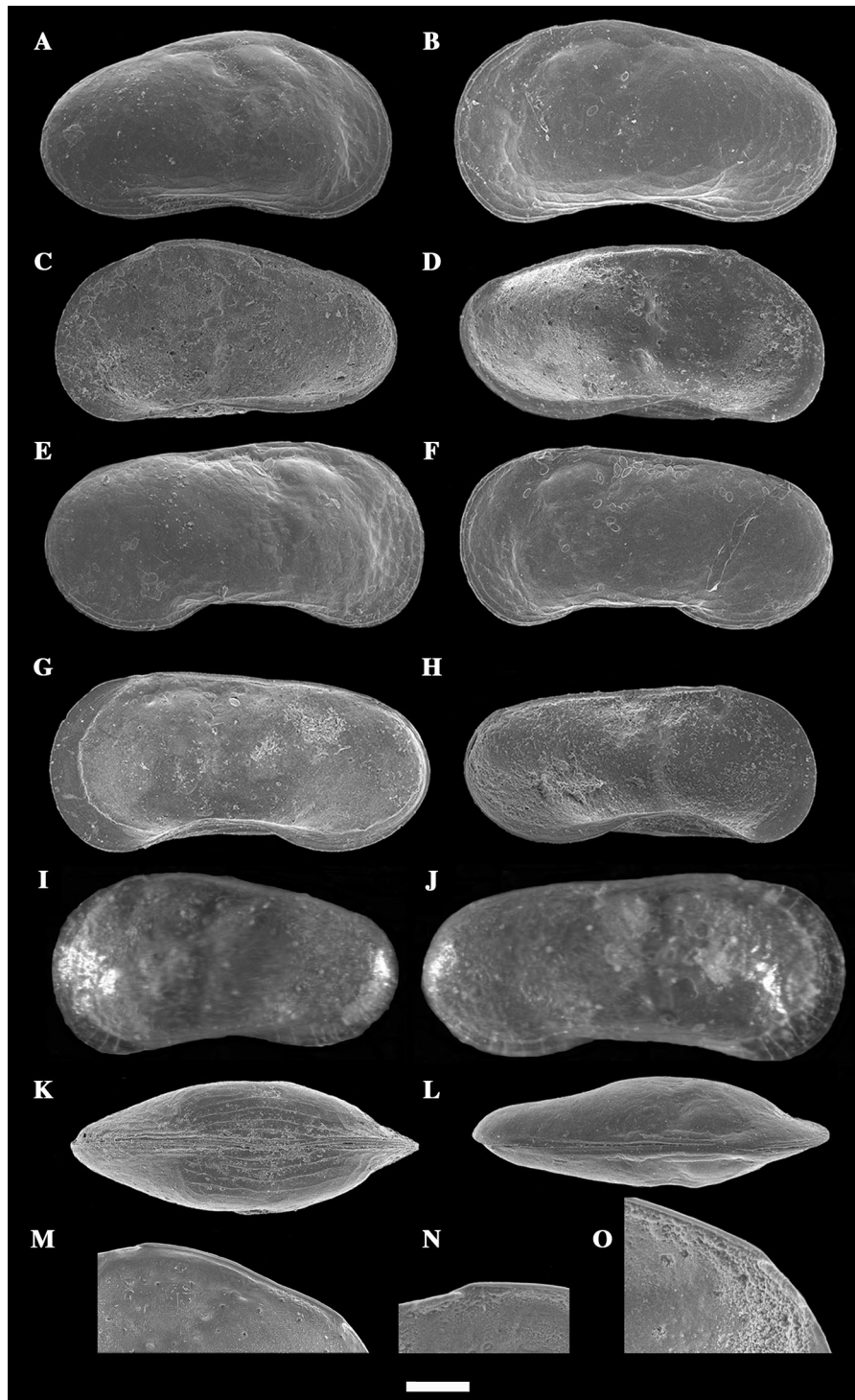
Description: Medium size. Carapace reniform to sub-rectangular in lateral view. Valves sub-equal with strong sexual dimorphism. Maximum height situated

approximately at the anterior 1/4 of the valves. In lateral view the anterior margin is broadly rounded and the posterior margin is sharply rounded. In dorsal view are depressed anteriorly and more globose in the posterior section. LV overlapping the RV in posterior margin.

Female valve in lateral view is reniform to sub-quadrate. Dorsal margin broadly arched, in some cases with a small hump coinciding with the maximum height in the anterior dorsal margin, anterior and posterior cardinal angles weakly discernible. Ventral margin slightly concave, incurved near the middle, with minimum height of the valve about 2/3 from the anterior margin.

Male valve in lateral view is longer and sub-rectangular. Dorsal margin straight, forming a soft angle when it reaches the anterior and posterior area. Ventral margin straight in the middle section of the





**Fig. 4** *Limnocythere* aff. *staplini*. **a** ♀ RV ev; **b** ♀ LV ev; **c** ♀ RV iv; **d** ♀ LV iv; **e** ♂ RV ev; **f** ♂ LV ev; **g** ♂ RV iv; **h** ♂ LV iv; **i** ♀ LV ev, light microscope illustrations showing the single undivided marginal pore-canals; **j** ♂ RV ev light microscope

illustrations showing the single undivided marginal pore-canals; **k** ♀ Cp vv; **l** ♂ Cp dv; **m** ♀ RV iv, hinge detail; **n** ♀ RV iv, anterior tooth detail; **o** ♀ RV iv, posterior tooth detail; scale bars **a–m** = 100  $\mu$ m; **n–o** = 50  $\mu$ m

valve, subparallel to dorsal margin, rounded towards the anterior and posterior region.

External valve ornamentation is a soft reticulation, in some cases completely absent, more developed in the margin's proximity. Four to five ribs develop around the anterior margin, starting approximately at the dorso-anterior hump and continuing in the ventral part, whereas in the posterior margin they are visible just around the margin. One median-dorsal transversal sulcus and one or two smooth, very poorly developed tubercles occur approximately at the anterior third of the maximum length. Normal pores scattered on the surface.

Internal view: Anterior and posterior margin rounded, ventral margin slightly curved inwards in the middle section, more marked approximately 2/3 from the anterior margin. Dorsal margin is straight in male and arched in female. Marginal zone well developed in the anterior, ventral and postero-ventral margins, but is two to three times larger in the anterior margin. Marginal pore canals undivided, straight.

The hinge is modified lophodont, antimerodont, consisting in the RV of a smooth groove with two terminal, one anterior and one posterior, medium-size smooth teeth. LV with a central smooth bar with an anterior and posterior smooth socket. Muscle scars as in genus. Juveniles are similar to adult females in contour, but a bit more rounded.

**Measurements of adults** Male: RV ( $n = 51$ ),  $L = 520\text{--}665\text{ }\mu\text{m}$  ( $604 \pm 33\text{ }\mu\text{m}$ );  $H = 242\text{--}300\text{ }\mu\text{m}$  ( $272 \pm 15\text{ }\mu\text{m}$ ); LV ( $n = 50$ ),  $L = 555\text{--}681\text{ }\mu\text{m}$  ( $614 \pm 33\text{ }\mu\text{m}$ );  $H = 240\text{--}310\text{ }\mu\text{m}$  ( $277 \pm 15\text{ }\mu\text{m}$ ). Female: RV ( $n = 92$ ),  $L = 512\text{--}662\text{ }\mu\text{m}$  ( $582 \pm 38\text{ }\mu\text{m}$ );  $H = 259\text{--}354\text{ }\mu\text{m}$  ( $302 \pm 22\text{ }\mu\text{m}$ ); LV ( $n = 95$ ),  $L = 514\text{--}684\text{ }\mu\text{m}$  ( $586 \pm 39\text{ }\mu\text{m}$ );  $H = 258\text{--}370\text{ }\mu\text{m}$  ( $301 \pm 22\text{ }\mu\text{m}$ ).

**Previous record in Argentina** The closely related *Limnocythere staplini* Gutentag and Benson, 1962 was originally described and found in North America (Gutentag and Benson 1962; Delorme 1971). Records of *L. staplini* in Argentina were later considered *L. cusminskyae* Ramón Mercau, Plastani and Laprida, 2014 (Ramón Mercau et al. 2014).

**Distribution in the Laguna Llanquanelo area and ecological data** Most (91%) *Limnocythere* aff. *staplini* specimens were found in Laguna Llanquanelo, a lentic mesosaline shallow waterbody subject to evaporation, with a mean annual salinity of 24.3 g

$\text{L}^{-1}$  and maximum salinity of  $42.3\text{ g L}^{-1}$ . The remaining 9% were collected from a small fresh to subsaline rheocene spring (Los Menucos), the Malargüe River delta, which forms small fresh to subsaline pools when joining the lake, and El Chacay and El Mocho creeks, both ephemeral, consisting of fresh to subsaline lentic and lotic sections. The species *Limnocythere* aff. *staplini* was absent in the fresh to subsaline helocene warm spring (Carapacho), in the subsaline limnocene springs (Carilauquen and La Porteña) and the freshwater lotic system of the Malargüe River.

**Remarks** Although more than 4500 individuals were studied, only hard parts were used in the description because the soft tissues were degraded. There are nine extant and Quaternary species of *Limnocythere* recorded in Argentina, but our specimens, utilising the morphology of hard parts and ecological preferences, is closest to *L. staplini*, known only from North America, although in general shape it is also comparable to *L. cusminskyae*, which is recorded in Buenos Aires Province, Argentina (Ramón Mercau et al. 2014). It is generally accepted that hard parts of ostracods are genetically determined, in particular the hinge morphology, as valves are the only available remains for fossil ostracod taxonomy (Gutentag and Benson 1962). Because our specimens show close similarity to *L. staplini*, we considered them to be *L. aff. staplini*, though the hinges show consistent differences among these three taxa. A taxonomic decision will be made once soft parts are available. It is not clear at the moment if *L. aff. staplini* is a new species or merely an ecophenotype of *L. staplini*, which if so, poses interesting biogeographic questions.

It is important to describe the differences in valve morphology among the three taxa. The hinge of RV of *Limnocythere staplini* has two crenulated terminal teeth and a strong depression in the median section of the dorsal region of the valve, whereas both teeth in *L. aff. staplini* are smooth and the depression in the dorsal region of the valves is soft or absent. Both teeth of the RV in *L. cusminskyae* are small, with the posterior being crenulated and the anterior smooth, with marked reticulation, and the presence of denticles on the anterior and posterior margins of the valves, absent in *L. aff. staplini*. Also, the dorsal margin of the valve in *L. staplini* and *L. aff. staplini* continues

with a symmetrical posterior curvature, in contrast to the dorsal margin in *L. cusminskyae*, which has a marked cardinal angle. With respect to ecological variables, *L. aff. staplini* is closer to *L. staplini*, preferring lentic saline water bodies.

## Statistical analyses

### Characterization of the water bodies from the Llanquanelo Basin

Environmental variables pH, salinity, dissolved oxygen, temperature, Ca, Mg, Ba, Sr, K and Na concentrations (ESM Table S1), measured seasonally at all sites, were analysed using cluster analysis to visualise factors that are stronger in segregation of the sampled localities (Fig. 5). Two main groups were separated. Group A includes environments with salinities  $>10.3 \text{ g L}^{-1}$  and group B includes sites with salinity  $<3.5 \text{ g L}^{-1}$ . Group A encompasses all the samples from Laguna Llanquanelo. Group B is segregated in two subgroups by K concentration, with subgroup B<sub>1</sub> characterized by K concentrations  $<5 \text{ mg L}^{-1}$ , grouping all samples from La Porteña spring, and most samples from Bañado Carapacho (warm spring) and Arroyo El Mocho; subgroup B<sub>2</sub>, with K content between 5 and  $113 \text{ mg L}^{-1}$  contains all samples from Los Menucos spring and most samples from the Río Malargüe delta, Arroyo El Chacay and Carilauquen spring.

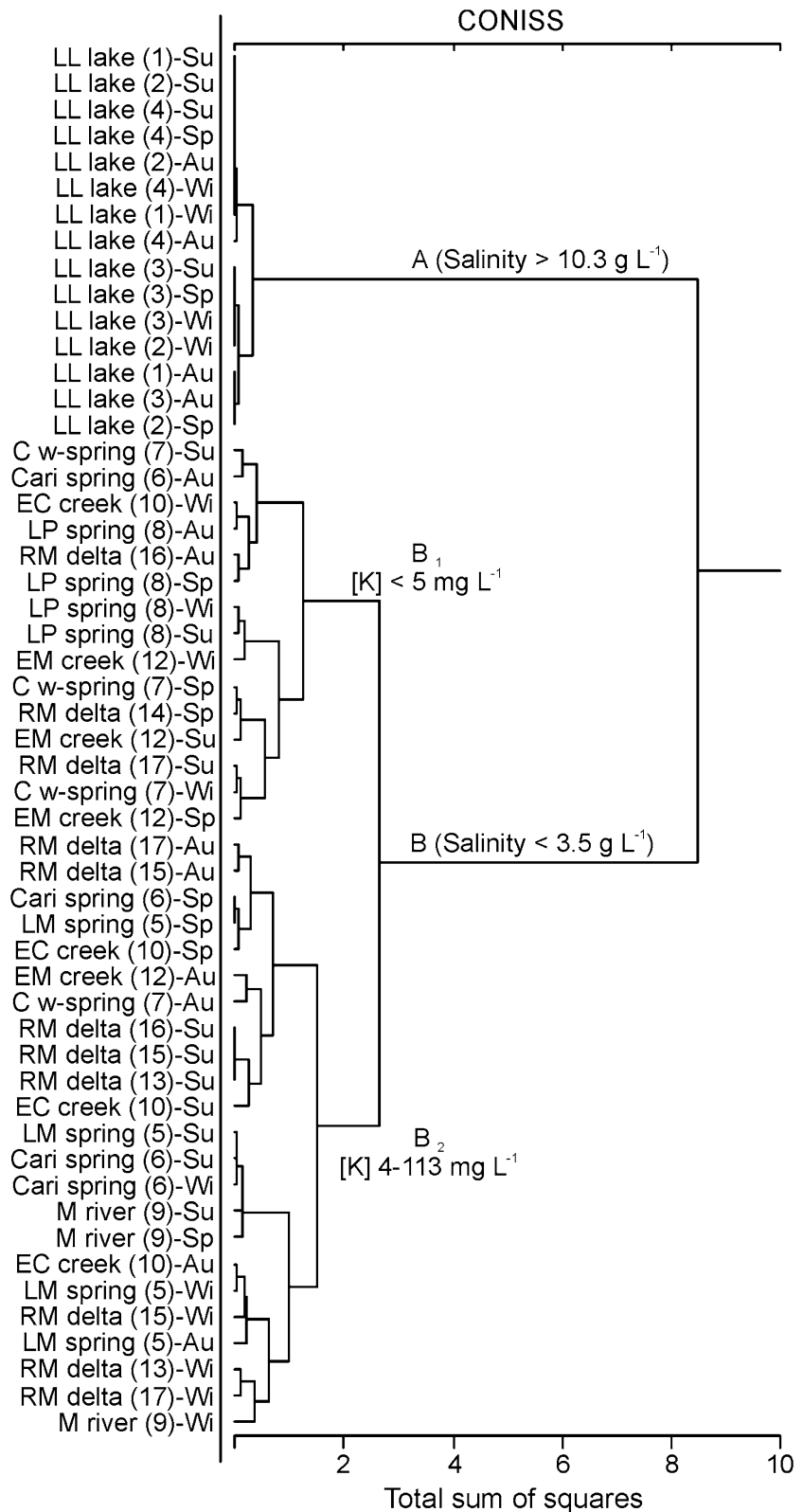
The relative abundance of ostracod taxa in the different ecosystems and the cluster analysis of their ecological preferences (Fig. 6) show two main components: (1) group A, formed by *Chlamydotheca* sp. and *C. arcuata* found only in the Carapacho warm spring, with a constant yearly temperature, and (2) group B, characterized by species with higher representation in seasonally dependent environments. Group B comprises subgroup B<sub>1</sub>, characterized by species that live almost exclusively in the springs and subgroup B<sub>2</sub>, characterized by species that live almost exclusively in lotic and lentic environments.

Subgroup B<sub>1</sub> is further segregated into B<sub>11</sub> with *P. incae* and *P. smaragdina*, which are almost exclusively represented in limnocrene and rheocrene spring environments, and B<sub>12</sub>, with *D. stevensoni*, which has 68% of its individuals living in the freshwater Bañado Los Menucos spring,

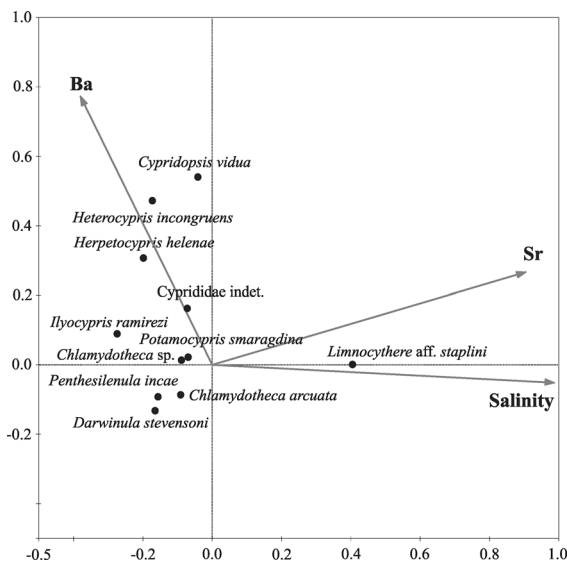
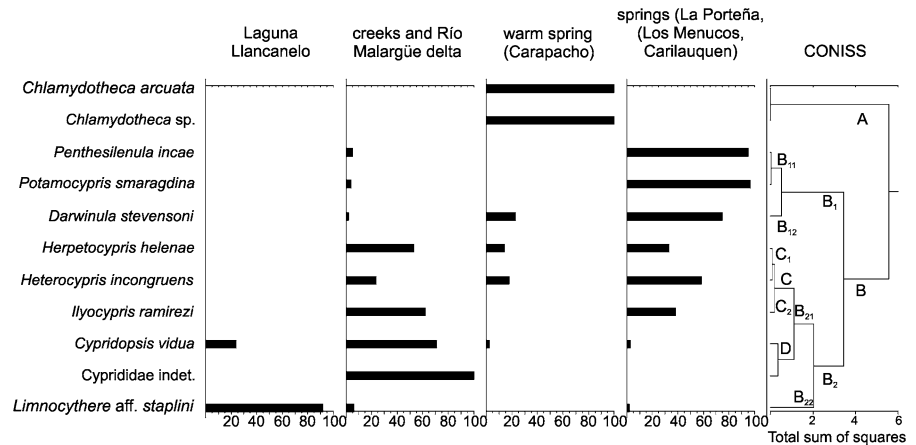
characterized by running water and 23% living in the Bañado Carapacho warm spring. Subgroup B<sub>2</sub> is further segregated into B<sub>21</sub>, characterized by species that live almost exclusively in lotic sites, but also present in springs, and in the case of *C. vidua*, also in the lake, and subgroup B<sub>22</sub>, represented by *L. aff. staplini*. Subgroup B<sub>21</sub> is further segregated into C and D. Subgroup C segregates further into C<sub>1</sub> with *H. helenae* and *H. incongruens*, both very plastic species that are present in all freshwater environments and C<sub>2</sub>, with *I. ramirezi*, with higher abundance in lotic environments. Subgroup D is characterized by Cyprididae indet., which is present only in lotic environments and *C. vidua*, with higher affinity to lotic environments, but also present in the saline lake.

In the Redundancy Analysis (RDA) (Fig. 7), the first two canonical axes explain 99.8% of the cumulative variance of species–environment relationships. The first canonical axis and the sum of all canonical axes explain a significant portion of the variance in the ostracod abundance data ( $p = 0.04$ ;  $p = 0.04$ , respectively). The environmental variables that were significantly correlated ( $p < 0.05$ ) with the canonical axes were salinity, Sr and Ba content. The concentration of K, Na, Ca, and Mg were removed because they were statistically co-linear. Salinity and Sr were correlated with the first axis ( $r = 0.99$  and  $0.90$ , respectively), while Ba was correlated with the second axis ( $r = 0.77$ ). Redundancy Analysis clearly defines two ostracod assemblages, determined by the environmental conditions. The first axis shows the gradient of salinity, with the highest values of this variable and Sr concentration in the positive sector with *Limnocythere* aff. *staplini*. The rest of the species are grouped in the negative quadrant of the first axis, indicating their preference for freshwater, with *C. vidua*, *H. incongruens*, *H. helenae*, *I. ramirezi*, *P. smaragdina*, *Chlamydotheca* sp. and Cyprididae indet. correlated with higher Ba concentration, whereas *P. incae*, *D. stevensoni* and *Chlamydotheca arcuata* show a weak negative relationship with Ba content. It should be noted that both *Chlamydotheca* species, despite being present only in the Carapacho warm spring, show different preferences for Ba; this is because *Chlamydotheca* sp. was found during spring and *C. arcuata* was found in both spring and autumn.

**Fig. 5** Cluster analysis of each sampling site in each season in relation to environmental variables. *LL lake* Laguna Llancanelo (Llancanelo Lake), *LM spring* Bañado Los Menucos (Los Menucos spring), *Cari spring* Bañado Carilauquen (Carilauquen spring), *C w-spring* Bañado Carapacho (Carapacho warm spring), *LP spring* Bañado La Porteña (La Porteña spring), *M river* Río Malargüe (Malargüe River), *EC creek* Arroyo El Chacay (El Chacay creek), *EM creek* Arroyo El Mocho (El Mocho creek), *RM delta* Delta del Río Malargüe (Malargüe River delta). The sampling site number is in brackets



**Fig. 6** Cluster analysis of ostracod species and their distribution in percentage in each type of environment



**Fig. 7** Redundancy analyses (RDA) diagram showing the correlation among eleven ostracod species and three environmental variables

## Discussion

Taxonomic analysis of ostracods from the Laguna Llançanelo area has extended the distribution range of all taxa, with some species exclusively found in this area. It shows that the assemblages are formed by taxa recorded only in the Arid Diagonal, but with others found in the subtropical Chaco-Pampean and/or Patagonian areas.

The species *Limnocythere* aff. *staplini* was the most abundant (>9700 recovered valves), lives mostly in ephemeral saline Laguna Llançanelo, and is described based on hard parts. *Limnocythere* aff.

*staplini* is very similar to *L. staplini*, known from North America (Canada, USA) (Gutentag and Benson 1962; Delorme 1971; Curry et al. 2012) and is also comparable to *L. cusminskyae* from the Argentinian Pampas (Ramón Mercau et al. 2014). Despite the similarities in valve shape and size, the hinges are clearly different, with the female RV having smooth and prominent anterior and posterior teeth in *L. aff. staplini*, both teeth crenulated in *L. staplini*, and the anterior tooth smooth and the posterior crenulated, both small, in *L. cusminskyae*. Delorme (1971) in a revision of the Family Limnocytheridae in Canada, indicated that the shape of the valve of *L. staplini* is very distinctive, which in part supports the notion that *L. aff. staplini* is a phenotypic variant, although the hinges are different as is the size, with valves of *L. aff. staplini* a little longer. Our specimens, however, are shorter compared with *L. cusminskyae*. A decision as to whether *L. aff. staplini* is a new species or an ecophenotype of *L. staplini* must wait until the study of soft tissues provides definitive evidence. *Limnocythere* aff. *staplini*, despite the disjunct distribution, has similar ecological and hydrochemical requirements as *L. staplini* [fresh to saline lentic waters of 0.2–43 g L<sup>-1</sup> (Forester 1983) and high concentrations of Ca (Curry et al. 2012), while *L. cusminskyae* prefers fresh to mesosaline salinity (0.5–20 g L<sup>-1</sup>) and bicarbonate-rich waters (Ramón Mercau et al. 2014)].

The species *Chlamydotheca arcuata*, originally described from temporary ponds and creeks (Díaz and Lopretto 2011), was recorded for the first time in a warm spring. The two species of *Chlamydotheca*, *C. arcuata* and *Chlamydotheca* sp. were found only in

the Carapacho warm spring, indicating a preference for relatively constant temperature (~20 °C). These taxa, however, were not found during winter, indicating that daylight, i.e. hours of insolation, may be the limiting factor. This confirms the value of seasonal collections when building a modern dataset, as it would not have been possible to establish that Carapacho had a constant, year-round warm temperature if only summer sampling had been done. Nor would it be possible to acquire information on ostracod species preferences and life cycles.

The main environmental factor segregating wetlands in the Llanquanelo area is salinity, with the evaporative saline lake set apart from all other freshwater wetlands (Fig. 5). Concentration of K is the factor that further separates the freshwater wetlands. When the analysis includes the ostracod taxa and their abundances, Carapacho warm spring is separated from the rest of the sites because it is the only locality with the two *Chlamydotheca* species found in the area. The creeks and saline lake are grouped together, separated from the other lentic freshwater sites. This is probably a consequence of the fact that the creeks are ephemeral and water is restricted to very shallow environments in both summer and winter.

The halophile association of Laguna Llanquanelo is characterized by abundant *Limnocythere* aff. *staplini*, which is present during all four seasons, accompanied by low numbers of *C. vidua* during the summer months. *Limnocythere* aff. *staplini* develops large populations, with 91% of its individuals living in the highly variable Laguna Llanquanelo. The species is also present in the rheocrene cold spring and creeks. Seventy-one percent of *Cypridopsis vidua* specimens were found in the creeks, and it is present in low numbers in Laguna Llanquanelo at salinities <29 g L<sup>-1</sup>. *Limnocythere* aff. *staplini* is absent in the warm spring and limnocrene spring and rare at other flowing freshwater sites, but is very abundant in the lake when salinity reaches 42.3 g L<sup>-1</sup> during summer. *Limnocythere* aff. *staplini* can be found in the lake at different water depths, commonly represented by large numbers of female, male and juvenile individuals. In this study, we also found that *L.* aff. *staplini* prefers higher concentrations of K, Na and Ca; and high levels of Sr and Mg (Table EMS S2).

The fresh water to subsaline ostracod assemblage is more diverse, characterized by the presence of

*Potamocypris smaragdina*, *Heterocypris incongruens*, *Chlamydotheca* sp., *C. arcuata*, *Penthesilenula incae*, *Darwinula stvensoni*, *Herpetocypris helenae*, *Ilyocypris ramirezi* and Cyprididae indet. The cosmopolitan species *H. incongruens* and *D. stvensoni* live in the freshwater springs and slow-flowing creeks. *Potamocypris smaragdina* and *P. incae* are restricted to freshwater, mostly in lentic environments, although the former is also present in the Río Malargüe delta. They can be considered stenohaline species, as indicated by Ramón Mercau et al. (2012), with *P. smaragdina* having affinity for lentic or low-current environments, whereas *P. incae* lives in environments with a constant freshwater supply (Cusminsky et al. 2011). *Ilyocypris ramirezi* has been found in cold springs and lotic environments, particularly the Río Malargüe delta, in fresh to subsaline (<3 g L<sup>-1</sup>) waters, but is absent in the lake. This does not support previous records describing it as 'euryhaline' (Markgraf et al. 2003; Schwalb et al. 2002; Laprida 2006; Ramón Mercau et al. 2012). The last authors suggested a salinity tolerance from freshwater to mesosaline for this species. The cosmopolitan species *D. stvensoni* and *H. incongruens* were found in cold and warm springs, as well as in the creeks, showing that these taxa tolerate a wide temperature range, contrary to Kulköylüoglu (2003), who associated *D. stvensoni* with mid-range temperatures, and Meisch (2000), who indicated a cold-water preference for *H. incongruens*.

## Conclusions

The 11 taxa of ostracods found in saline Laguna Llanquanelo and related freshwater wetlands can be considered moderately diverse, and the number compares well with the fifteen taxa described from northern Patagonia and 12 from southern Patagonia (Ramón Mercau et al. 2012). This study shows that *Herpetocypris helenae*, *Limnocythere* aff. *staplini*, *Chlamydotheca* sp. and the undetermined Cyprididae are restricted to the Laguna Llanquanelo area.

The 'subtropical' taxon *Chlamydotheca arcuata*, with exclusive American distribution, and *Penthesilenula incae*, found in Neotropical areas, were previously recorded in Argentina only in wetlands from the Puna (northwest Argentina) and Patagonia. *Potamocypris smaragdina*, a taxon with Palearctic–



Neotropical distribution and cosmopolitan *Darwinula stvensoni* and *Heterocypris incongruens*, have been found in both the Pampean and Patagonian areas, together with the endemic *Ilyocypris ramirezi*.

This study shows that *Limnocythere* aff. *staplini* is a euryhaline taxon, indicative of shallow, saline water bodies that are subject to changes in salinity and temperature, and also related to Na, K, Sr and Ca in the water. Other taxa, except *C. vidua*, are typically from freshwater, in some cases showing affinity to Ba content (*C. vidua*, *H. incongruens*, *H. helenae*, *I. ramirezi*, *P. smaragdina* and Cyprididae indet.). After salinity and ionic composition of the water, temperature and pH are the ecological variables that influence these ostracods. At present, arid conditions characterize the area, with extensive salt crusts deposited around Laguna Llanquanelo. These freshwater bodies serve as refuges for species that cannot tolerate higher salinity.

Our data suggest that *Limnocythere* aff. *staplini*, *Herpetocypris helenae*, *Chlamydotheca* sp. and the Cyprididae indet. are found only in the Arid Diagonal, though more studies are needed to confirm the endemic nature of these taxa. This work provides the first modern database of ostracods and water chemistry (with SEM images, water variables, and seasonal data) from South America. Additional data from other South American regions will provide information to construct a continental dataset that can be applied to ostracods in quantitative paleolimnological and paleoclimatic reconstructions, and can be compared with Northern Hemisphere reconstructions to better understand biogeographic patterns. Despite the preliminary nature of this database, this study provides modern analogue data needed to infer past climate and ecological conditions on the continent, particularly in the Laguna Llanquanelo area where a multidisciplinary paleolimnological study is underway.

**Acknowledgements** We thank the Dirección de Recursos Naturales de la Provincia de Mendoza for facilitating the research on this Ramsar site. We also thank park ranger Fabricio Ayala for his invaluable help in the field. We thank Silvina Lassa, Nick Mackie and Rafael Urréjola for technical assistance with the SEM. The assistance of David Wheeler and Lili Yu at the University of Wollongong is greatly appreciated. This work was supported by a grant from the Agencia Nacional de Promoción Científica y Tecnológica, FONCYT (Argentina) (Grant Raíces 2006 – PICT 1311), which also enabled DSD to take a visiting position in Wollongong.

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